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THE RELATION BETWEEN REGULATION AND FISSION IN PLANARIA.

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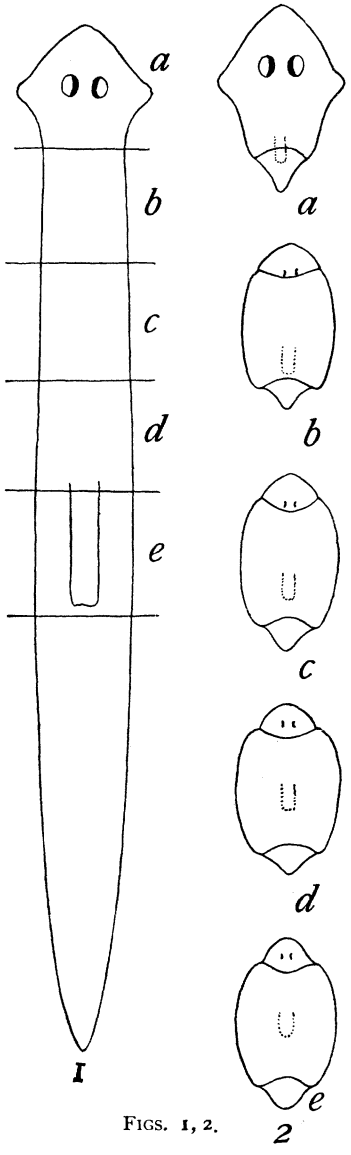
The data discussed below were obtained at various times during the last five years from two species of *Planaria*, *P. maculata* and an unnamed Californian species differing from *P. maculata* in color, length of "auricles" and length of pharynx (Fig. 8), but resembling it very closely as regards regulation and fission.

I. THE POSITION OF THE PHARYNX IN PIECES FROM DIFFERENT LEVELS.

It has been known since Morgan's experiments on *Planaria maculata* that the position of the newly formed pharynx in a piece differs according to the level of the body from which the piece was taken. According to Morgan the new pharynx arises posterior to the middle of the piece in prepharyngeal pieces, its distance from the middle decreasing as the level of the piece approaches the pharyngeal region of the original animal; as regards postpharyngeal pieces, however, he states merely that the pharynx arises anterior to or near the middle of the piece. My own observations on prepharyngeal and pharyngeal pieces agree with his. Figs. 1 and 2, *a–e*, indicate this relation between level and pharyngeal position. The regulation of postpharyngeal pieces, however, presents a number of important features, which Morgan has not, so far as I am aware, described. If the whole postpharyngeal region be cut off as one piece, the new pharynx always arises a considerable distance anterior to the middle (Fig. 3) its position varying somewhat in different cases. If, however, this region be cut into several pieces (Fig. 4, *a*, *b*, *c*, *d*)

we find that the new pharynx appears anterior to the middle in pieces from the anterior part of the postpharyngeal region and at or very near the middle in pieces from the posterior portion (Fig. 5, *a*, *b*, *c*, *d*); in other words *the distance between the new pharynx and the anterior end increases with increasing distance from the old pharyngeal region.* By analogy with the prepharyngeal region we should expect just the opposite, but in only two cases out of more than a hundred have I seen it (Figs. 6 and 7, *a*, *b*, *c*). In these two cases *the distance between the new pharynx and the anterior end of the piece decreases with increasing distance from the old pharyngeal region.*



FIGS. 1, 2.

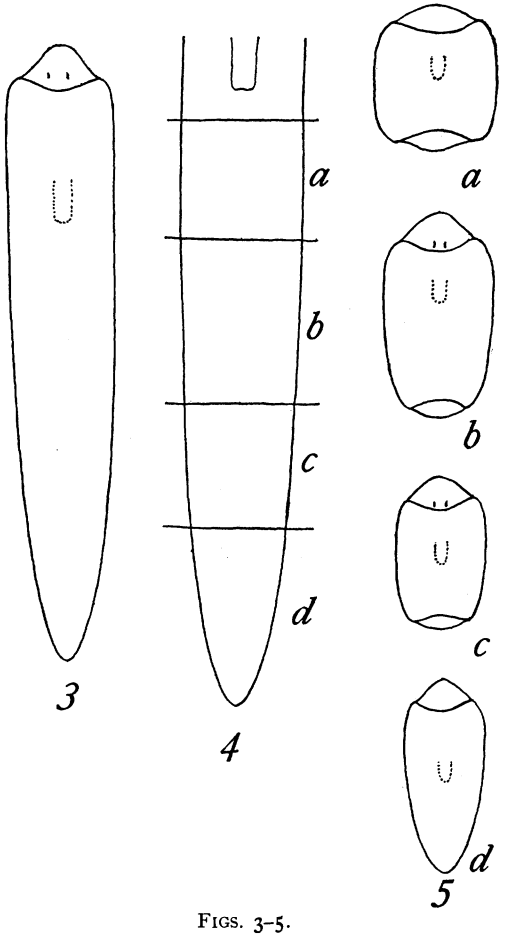
It is necessary here to refer very briefly to certain interpretations suggested in previous papers.[1] According to these suggestions the course of regeneration in a piece will depend very largely upon its past associations with the various functional

[1] "Studies on Regulation — IX., The Position and Proportions of Parts During Regulation in Cestoplana in the Presence of the Cephalic Ganglia," *Archiv f. Entwickelungsmech.*, Bd. XX., H. 1, 1905.

"Studies on Regulation — X., The Positions and Proportions of Parts During Regulation in Cestoplana in the Absence of the Cephalic Ganglia," *Archiv f. Entwickelungsmech.*, Bd. XX., H. 2, 1905.

"Contributions toward a Theory of Regulation — I., The Significance of the Different Methods of Regulation in Turbellaria," *Archiv f. Entwickelungsmech.*, Bd. XX., H. 3, 1906.

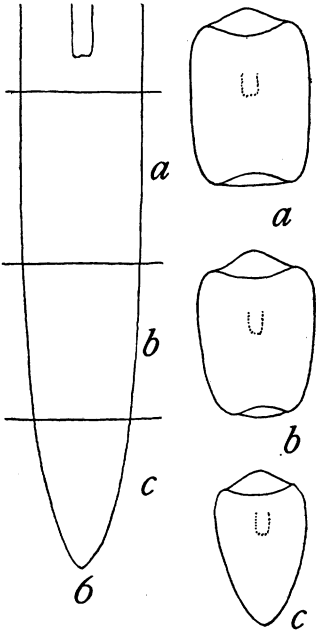
complexes of the whole, thus a piece from the anterior regions of the body is functionally much more "anterior" than a piece from the middle of the body; consequently in the new wholes formed from these pieces we shall find relative differences in size of various parts. In the "anterior" piece, for example, the anterior region will be much larger than the posterior and in the piece from the middle of the body the two will be about equal.



FIGS. 3–5.

In normal animals the pharynx is situated in the middle of the body but in those new animals formed from the pieces the physiological or functional middle does not coincide with the

structural middle: in anterior pieces the functional middle is near the posterior end; in pieces from the middle of the body it is near the middle, etc. The new pharynx appears at this functional middle or as we may more properly call it the physiological pharyngeal region. With this interpretation in mind the difference in position of the pharynx in the pieces *a–e*, Fig. 2, is readily understood.



FIGS. 6, 7.

Now we might expect that pieces from the postpharyngeal region would show relations similar in character but reversed, *i. e.*, a decrease in size of the new prepharyngeal region with increasing distance from the pharynx. As a matter of fact just the opposite occurs (Figs. 4, 5, *a*, *b*, *c*, *d*) except in very rare cases (Figs. 6 and 7) so that the prepharyngeal and postpharyngeal regions are usually equal in size in pieces from the extreme posterior end.

We must conclude from this relation that pieces such as *c* and *d* in Fig. 5 are physiologically more anterior than pieces *a* and *b*. I believe that the occurrence of fission affords a very simple explanation of these facts. It is highly improbable that fission occurs in these forms without some physiological preparation even though changes in structure may not be visible. Various authors have noted that fission in certain other turbellaria is initiated by changes in the nervous system leading to the development of new cephalic ganglia. If such changes are going on in this postpharyngeal region in *Planaria* there is no difficulty in understanding why the new prepharyngeal region should be longer in these pieces than in those farther anterior. Moreover,

I do not believe that any other explanation of these remarkable facts can be found.

The two exceptional cases noted above (Figs. 6, 7, *a*, *b*, *c*) were from worms captured through the ice in January when food was scarce and activity slight on account of the low temperature and hence in all probability no preparation for fission existed. These cases only serve, therefore, to render more probable the interpretation given above.

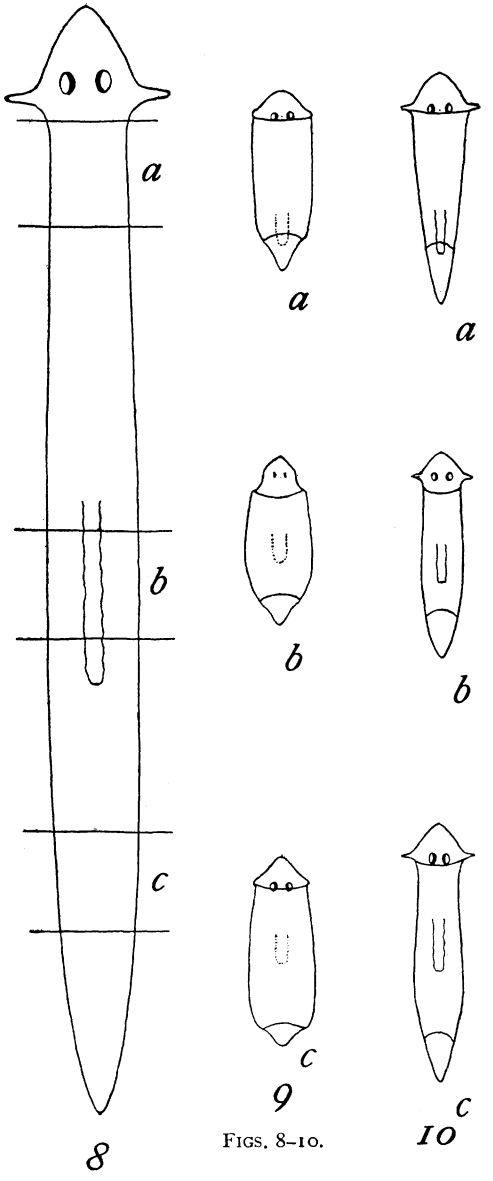
In *P. simplicissima*, which is not known to undergo fission the relative position of the pharynx in pieces as from different levels is, according to Morgan, similar to that in the winter specimens of *P. maculata*.

II. The Size of the Head at Different Levels.

In 1901 I first noticed that the new head formed was larger in pieces from the anterior part of the prepharyngeal region and from the posterior half or two thirds of the postpharyngeal region than in pieces from the middle region of the body. Moreover, in the pieces from the middle region a considerable amount of new tissue is formed posterior to the eyes while in the anterior and posterior regions the eyes lie almost in the plane of the cut surface.

If we cut the whole body into equal pieces and compare them we find the size of the head decreasing and the distance between the eyes and the cut surface increasing as we proceed posteriorly toward the old pharyngeal region. Pieces just anterior or posterior to or in the pharyngeal region are much alike, all forming relatively small heads and relatively long "necks" of new tissue. In the postpharyngeal region, however, the size of the head increases and the length of the neck decreases until in the posterior half of the postpharyngeal region the head is about as large as in anterior pieces and the eyes appear in the plane of the cut. Both species of *Planaria* are similar in this respect. Figs. 8, 9 and 10, *a*, *b*, *c*, illustrate the case under consideration. Fig. 8 indicates the regions from which the pieces *a*, *b* and *c* were taken; in Fig. 9, *a*, *b*, *c*, the difference in size of the head and length of the "neck" in the new tissue is shown at an early

stage of regulation and in Fig. 10, *a*, *b*, *c*, at a later stage. These figures as well as all my conclusions on this point are based on



FIGS. 8–10.

careful and repeated measurements of all pieces, although the difference is sufficiently striking without such aids.

I believe that these differences are also indicative of the physiological conditions at different levels. In previous papers [1] I have suggested that the relation between redifferentiation and regeneration proper depends upon the physiological differentiation of parts. As the difference in physiological or functional specification between the part removed and the part remaining increases the amount of redifferentiation decreases and that of regeneration increases up to a certain limit and vice versa. To take a concrete case: the more "head-like" in the physiological sense the anterior portion of a piece of *Planaria* is, the smaller the amount of new tissue formed at this end and the greater the amount of redifferentiation. Now the anterior ends of pieces from the anterior regions of the body of *Planaria* and those from the posterior half of the postpharyngeal region are visibly more "head-like" than those of pieces from the middle region. This is evident from the degree and character of their activity. Correspondingly we find that only the part anterior to the eyes is formed by regeneration, the "neck" and in some cases the auricles themselves being formed by redifferentiation in the pieces from anterior and posterior regions (Figs. 9, *a*, *c*, and 10, *a*, *c*). On the other hand, in the pieces from the middle region not only the head but a longer or shorter "neck" is formed by regeneration.

The difference in size of the heads furnishes more evidence along the same line. The greater the relative intensity of a given functional complex the larger the relative size of the structural complex which represents it. Hence the more "head-like" a given piece is the larger the relative size of the head formed and vice versa (cf. Figs. 9, *a*, *b*, *c*, and 10, *a*, *b*, *c*).

The conclusions from this line of evidence are the same as those reached from a comparative study of pharyngeal position *viz.*, that in the posterior half or two thirds of the postpharyngeal region a marked increase in the functional conditions charac-

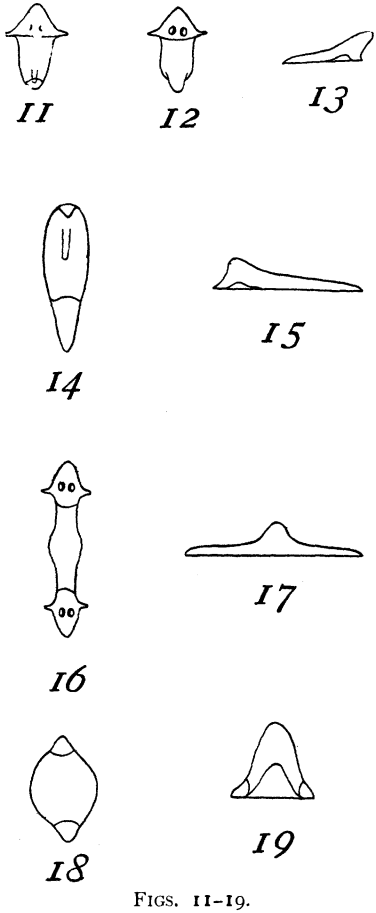
[1] "Studies on Regulation — VIII., Functional Regulation and Regeneration in Cestoplana," *Archiv f. Entwickelungsmech.*, Bd. XIX., H. 3, 1905.

"Contributions toward a Theory of Regulation — I., The Significance of the Different Methods of Regulation in Turbellaria," *Archiv f. Entwickelungsmech.*, Bd. XX., H. 3, 1906.

teristic of the anterior region occurs — that is the change is due to the development in this region of a new "head" physiologically speaking.

III. Regulation in Very Small Pieces.

By the use of pieces approaching the minimal size in which regulation is possible, we have a means of determining the physiological potences of the various regions more exactly than by any other method. I have recorded the full history of a large number of species of this kind from both species of *Planaria*, though mostly from the Californian.



Figs. 11–19.

Worms of rather large size were selected and cut into eighteen to twenty pieces by transverse or nearly transverse cuts. Each piece was numbered and isolated and observed as an individual. The results of these experiments are rather remarkable. The pieces from the region immediately posterior to the old head produce a large head and a very small posterior end with the pharynx near the latter (Fig. 11) or sometimes no pharynx, *i. e.*, these pieces are so exclusively "anterior" physiologically speaking that sometimes they are incapable of giving rise to the pharyngeal and postpharyngeal regions at all, and in any case these regions are small. The pieces behind these show a smaller head and larger posterior end with the pharynx approaching the middle and give rise to normal animals. But a region including the old pharynx and extending for a short distance anterior and posterior

to it affords a remarkable variety of results in these small pieces. Five different methods of regulation occur: (1) The piece may form a normal animal; (2) it may be fully used up in the formation of a head and anterior region without a pharynx or postpharygneal region (Fig. 12). In such cases a dorsal thickening occurs in the posterior region (Fig. 13, optical section in median plane); (3) the piece may go entirely to the formation of a posterior region without head and with or without pharynx (Fig. 14). Such pieces bear a dorsal thickening in the anterior region (Fig. 15); (4) the piece may form a head at each end (Fig. 16). In these cases there is a dorsal thickening in the middle (Fig. 17); (5) the pieces may form a tail at each end (Fig. 18). Such pieces acquire after two or three weeks the outline shown in Fig. 19 in consequence of the opposed activity of the two posterior ends.

The cases 3 and 4 have been described by Morgan and others but so far as I am aware cases 2 and 5 have not been recognized as what they actually are, though they have undoubtedly been seen by many observers and grouped with abnormalities. The pieces from the postpharyngeal region almost without exception produce normal animals. Occasionally a case of double heteromorphic heads like Fig. 16 occurs very near the extreme posterior end of the body, often in next to the last piece.

Thus the middle region as compared with the anterior and posterior regions appears to be indifferent; pieces from it may form single or double anterior parts, or single or double posterior parts, or normal animals. The different possibilities do not occur in any definite order; a single or double "tail" is as likely to follow a double "head" as is a normal animal and *vice versa*. Neither does the presence of the old pharynx play any part in the production of these various results, for the region where they occur most frequently begins some distance anterior to the pharynx and ends some distance posterior to it.

I believe that we must consider this region as physiologically indifferent, *i. e.*, neither "anterior" nor "posterior" in the functional sense to any marked degree. In consequence of this indifference the actual course of regulation must depend on slight chance internal differences in the pieces. If one end becomes pbysiologically dominant the piece may give rise to a single

"head" or a single "tail." If both ends maintain their independence a normal animal or double "heads" or double "tails" may result according as the physiological conditions are different or alike. The dorsal thickening in these cases of partial animals represents that region of the body toward which the intestinal contents are forced during contraction. It is caused by the formation of an intestinal cavity in this region in consequence of the pressure and this cavity continually enlarges in the direction of least resistance, *i. e.*, directly dorsally (Figs. 17 and 19) or dorso-posteriorly (Fig. 13) or dorso-anteriorly (Fig. 15) as the case may be. As the size of the pieces from this region increases normal animals are more frequently formed until beyond a certain limit all pieces give rise to normal animals.

At present I desire chiefly to call attention to the fact that the two regions separated by this indifferent region resemble each other in regulation since they usually produce normal animals. We might expect from their position in the body to find the pieces from the post-pharyngeal region predominately "posterior" in function. but as a matter of fact they show "posterior" and "anterior" characteristics in equal degree since prepharyngeal and postpharyngeal regions are of the same size. Here again the only satisfactory explanation of the facts is the existence of the early stage of individualization of a new head region somewhere in this postpharyngeal region. The results with small pieces indicate that this condition is not sharply centralized or localized in the region but extends more or less completely throughout its length. Moreover, the remarkable agreement of these different lines of evidence when considered from the point of view adopted in this paper affords an indication of the value of this point of view as a means of interpretation and unification of the mass of data which have accumulated in this field.

I believe that the supporters of theories of regulation based on formative substances or upon "entelechies" will find a certain amount of difficulty in interpreting some of the facts cited here, but discussion of my conception of their bearing is postponed.

As is well known, fission in *Planaria maculata* occurs in a region some distance posterior to the pharynx and the same is

true of the Californian species. My observations have led me to believe, however, that the level varies to a considerable extent. The direct cause of separation seems to me to be a difference in reaction of the two parts; a certain portion of the postpharyngeal region attaches itself firmly while the other parts of the body attempt to move forward. Since the motor power for the forward movement, *i. e.*, the cilia and the margins of the body — is applied not at the anterior end only but throughout the whole length of the part anterior to the attached region the greatest strain will occur just anterior to the attached region and rupture will occur here even in the absence of any preformed zone of weakness. Personally I am inclined to doubt the existence of any such zone of weakness, but I think the facts show very clearly that under ordinary conditions *Planaria* consists physiologically of two zoöids.

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